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A SCENARIO FOR THE EVOLUTION OF SOCIAL ORGANIZATION IN RUFFS *PHILOMACHUS PUGNAX* AND OTHER CHARADRIIFORM SPECIES

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1. INTRODUCTION

The pigeon's wing and the penguin's wing can easily be distinguished from each other. Their outer appearance is very dissimilar and their primary use completely different. Pigeons utilize their wings for flying through the air, penguins for diving in the water. Yet, fossil remains from all kinds of extinct bird species strongly suggest that both wing types can be derived from one and the same primitive structure in the early birds from the Jurassic or Cretaceous. Consequently, both wing types can be considered to be homologous patterns in birds.

The pigeon's wing and the bat's wing do not differ with respect to their primary use. Both types are employed for flying through the air. Morphological features of these two recent wing types and fossil remains from all kinds of extinct vertebrates emphasize that they cannot be derived from the same primitive wing pattern. Hence, both types of wings can be considered to be analogous structures which converged from a different phylogenetical origin.

Fossil remains may be of great help in tracing phylogenetical relations between species and morphological structures. Such sources of evidence can rarely be used in the study of the phylogeny of behaviour and of social organization. Consequently, phylogenetical approaches of social organization in birds have not been undertaken very often, although general theories concerning the evolution of sociality (e.g. Wilson

1975) receive a rapidly growing attention. Nevertheless, it has been shown (e.g. Kear 1970) that new insights may be obtained by phylogenetical approaches of social organization based on precise behavioural comparisons between species of which phylogenetical relations have independently been established.

In this paper an attempt will be made to trace the evolutionary roots of social behaviour in the Ruff *Philomachus pugnax*. In an earlier paper (Van Rhijn 1983) a number of suggestions have been made regarding this topic. This paper adds no new data about the Ruff's social system, however, its main purpose is to develop a theory about the derivation of such systems from an early ancestor which also established a group of birds (subfamily Calidridinae, family Scolopaciidae, order Charadriiformes) with an extremely large variety of social systems. Thus, the most important difference with the previous paper is a considerable increase in the magnitude of the reference group for comparisons.

2. SOCIAL ORGANIZATION IN THE RUFF

In spring male Ruffs gather on traditional leks which are also visited by females of the species, the Reeves (Bancke & Meesenburg 1952, 1958, Siedel 1960, Hogan-Warburg 1966, Spillner 1971, Van Rhijn 1973, Shepard 1975). Most courtship and mating occurs on these leks. In a lek community certain males, named resident males, defend small bare spots of ground or residences in the meadow. On the border of a lek some other males, named marginal males, may try to obtain a residence. Roles between resident and marginal males are interchangeable. Therefore they are classified together as independent males. These males exhibit a high proportion of fighting and threat in their behaviour. They normally possess dark coloured nuptial plumages.

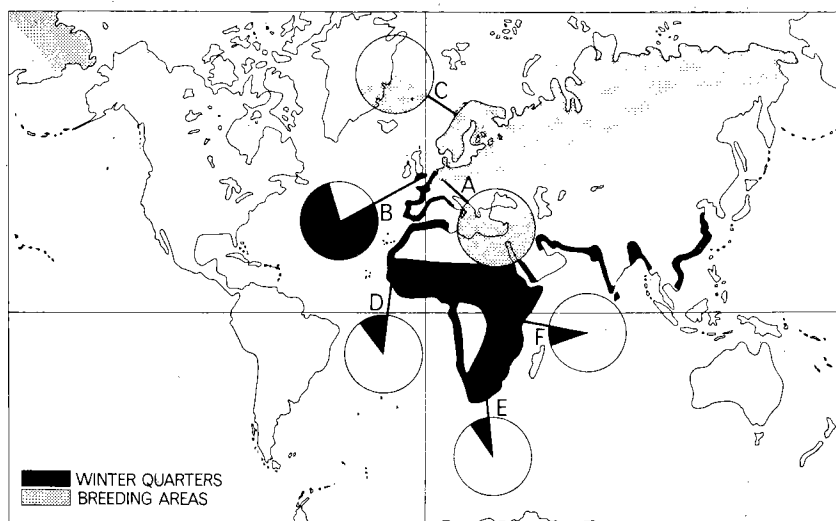


Fig. 1. Breeding and wintering areas of the Ruff after Glutz *et al.* (1975) and Cramp & Simmons (1983), and the proportion of males in The Netherlands (A: Pieters *et al.* 1967, Koopman *et al.* 1982), in England (B: Greenhalgh 1968), in Finland (C: Saurola 1977), in Senegal (D: Morel & Roux 1966), in South Africa (E: Schmitt & Whitehouse 1976), and in Kenya (F: Pearson 1981).

Certain other males, named satellite males, rarely fight or threaten. Satellites, which mainly possess light or white coloured plumages, are tolerated on the residences and may be equally successful in mating as independent males (Van Rhijn 1983). Bij observing individuals over successive seasons, strong evidence has been obtained that a male adopts either the independent or the satellite role for his whole life. It is very likely that genetical factors are associated with this role-differentiation (Hogan-Warburg 1966, Van Rhijn 1973, 1983).

As in many other waders (Myers 1981a, b) Ruff and Reeve migrate in different times of the year. Furthermore, from data on sex-ratio (Fig. 1) it seems as if males and females have different distribution areas during winter and summer. In The Netherlands the average proportion of males is 67%. Even a higher proportion of males was found in wintering and migrating flocks in England: 80%. In Finland, however, male proportion in all Ruffs caught for ringing was only 33% and in the African winter quarters male proportion turned out to be extremely low: 10% in Senegal, 9% in South Africa, and 7% in Kenya. These data suggest that male Ruff do not migrate every year very far from the southern breeding areas.

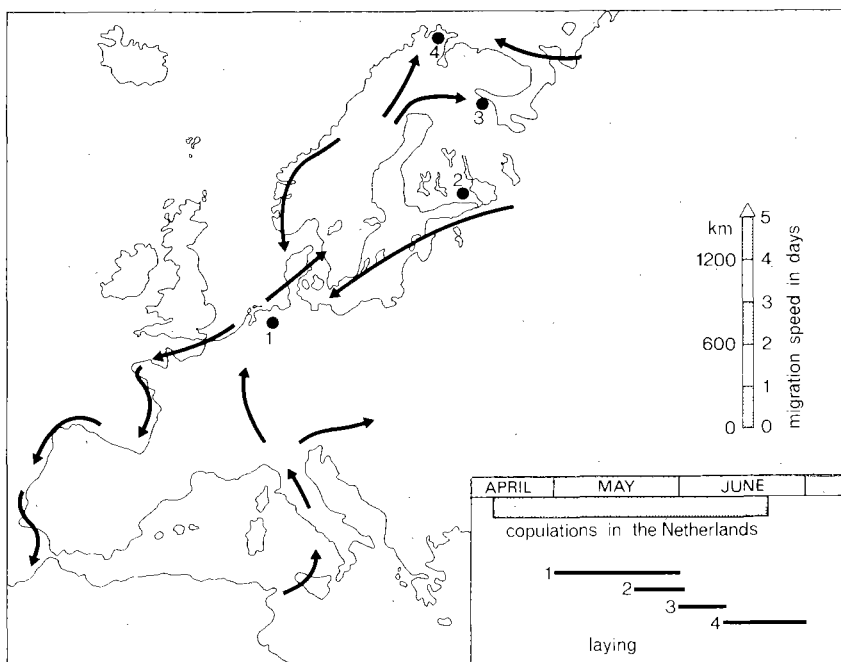
Two times every year females have to cross these southern breeding grounds. If they would stay for some period of time, their passing should be associated with changes in the sex-ra-

tio. Data collected on migrating Ruffs in The Netherlands (Koopman *et al.* 1982) show that during most of the year the proportion of males is very high: about 80%. Indeed, during two short periods this proportion may drop to approximately 50%. These two periods from the end of April up to the beginning of May and the first part of August coincide with a high migratory activity, as indicated by peaks in the number of trapped birds (Koopman *et al.* 1982).

Direct observations in the field also suggest a large discrepancy between the number of Reeves visiting and copulating on leks and the number of nesting Reeves (Van Rhijn 1983). In The Netherlands the number of copulating Reeves is much higher than the number of males displaying on leks, and the number of nesting Reeves seems to be much lower. Since the Dutch leks, apart from belonging to the most southern part of the breeding range, are situated along an important migration route of the Ruff (Fig. 2), I suggested that many of the Reeves observed copulating in The Netherlands continue migration.

Eventual success of a copulation depends on the survival of fertile spermatozoa until ovulation of the egg. Ovulation occurs about one day before egg-laying. Fertility of the spermatozoa of birds is maintained for at least 7 days in all species which have been studied. In the domestic chicken most eggs are fertilized within 12 days after the last copulation and in the do-

Fig. 2. Migration routes of the Ruff in western Europe, migration speed, copulation period in The Netherlands, and laying periods in The Netherlands (1), southeast Finland (2), and two areas in northwestern Europe (3 and 4) compiled from Glutz *et al.* (1975) and own observation.



mestic turkey even up to 28 days (Lake 1975). In the uterovaginal sperm-storage glands of female petrels (Procellariiformes) fertility of spermatozoa may last even up to eight weeks (Hatch 1983). I have seen copulating Ruffs in The Netherlands from 20 April up to 10 June. Egg-laying in the north of Europe and Siberia mainly occurs during June (Glutz *et al.* 1975). Migration from The Netherlands up to the north of Scandinavia may last only 7 days, assuming an average speed of 300 km/day (Glutz *et al.* 1975). Consequently, there is no reason to reject the possibility that some of the copulations of migrating Reeves induce fertilization (Fig. 2).

Copulation on migration has been brought in relation with the food conditions in the extreme north of the breeding range (Van Rhijn 1983). The numerous small prey items offer favourable conditions for chicks. For the male Ruff, however, as the largest calidridine sandpiper, much time might be needed for collecting the large number of food items to cover his energetic requirements. This could imply that there are strong limitations on the opportunities for other activities, such as inter-male competition on leks. It therefore seems that the northern breeding areas are not very attractive for males. Only

those individuals which fail in the competition for copulations on leks, might adopt other strategies (Gadgil 1972) and migrate further to the north in spring. This could explain why, in contrast to Bergmann's rule, males from northern Europe (Swedish Lapland) have smaller body measurements than males from the middle of Europe (Glutz *et al.* 1975), although an alternative explanation has been proposed for this phenomenon (Salomonsen 1955).

3. SOCIAL ORGANIZATION IN OTHER WADERS

The Ruff's social system is characterized by 1) lek behaviour, 2) role differentiation between males, and possibly 3) a temporal and spatial segregation between copulation and fertilization. Lek behaviour is shown by at least two other related species: The Buff-breasted Sandpiper (*Tryngites subruficollis*: Prevett & Barr 1976, Myers 1979) which is a member of the same subfamily Calidridinae (Voous 1973) and the Great Snipe (*Gallinago media*: Lemnell 1978) which is a member of the same family Scolopacidae. Within the other Charadriiformes no other species are known with lek systems, although in a limited number of additional species promiscuity or polygyny predominates. These

latter kind of mating systems occur in four members of the Calidridinae: *Calidris fuscicollis*, *C. melanotos*, *C. accuminata*, and *C. ferruginea* (Pitelka 1959, Holmes & Pitelka 1964, Parmelee *et al.* 1968, Pitelka *et al.* 1974, Myers 1981a, 1982, Myers *et al.* 1982); and in some other members of the Scolopacidae: e.g. the American Woodcock (*Scolopax minor*: Pitelka 1943) and the Eurasian Woodcock (*Scolopax rusticola*: Hirons 1980). Predominantly promiscuous or polygynous mating systems have not been described for other families of the order Charadriiformes (Table 1).

Permanent role differentiation between males has not been described for any other species within this order. Similarly, a temporal and spatial segregation between copulation and fertilization has never been suggested for related species. On the contrary, presence of motile sperm

in the uterovaginal sperm-storage glands of female American Woodcock shot in January or February in their winter quarters in Alabama was interpreted as local breeding (Walker & Causey 1982). Nevertheless, several sandpiper species display elaborate courtship (probably not including copulation) in their winter quarters and during spring migration (e.g. *Tryngites subruficollis*: Oring 1964, Myers 1980) or close to their breeding areas before nesting territories can be occupied (e.g. *Calidris bairdii*: Myers *et al.* 1982). Early courtship in these species, however, has never been proposed to result in fertilization during migration.

Monogamous pair bonds predominate in the great majority of Charadriiform species. Throughout this order the males of most species fulfill an important role in incubation and care for the chicks. In a considerable number of spe-

Table 1. Phylogenetic classification of recent Charadriiformes after Cracraft (1981), climatological and geographical distribution of families after Larson (1957) and Van Tyne & Berger (1975), and the incidence of species with predominantly polygynous or promiscuous mating systems, and of species in which almost all parental care is performed by the males

	climate	hemisphere	polygyny	paternal care
suborder Alcae				
family Alcidae	cold	north		
suborder Charadriomorpha				
infraorder Dromae				
family Dromadidae	warm			
infraorder Lari				
superfamily Stercorarioidea				
family Stercorariidae	cold			
superfamily Laroidea				
family Rhynchopidae	temperate/warm			
family Laridae	cold/temp/warm			
infraorder Chionae				
family Chionidae	cold	south		
family Thinocoridae	cold/temp	south		
infraorder Burhirni				
family Burhirnidae	temp/warm			
infraorder Charadrii				
superfamily Haematopodoidea				
family Haematopodidae	temp/warm			
family Recurvirostridae	temp/warm			
superfamily Charadroidea				
family Glareolidae	warm			
family Vanellidae	temp/warm			
family Charadriidae	cold/temp/warm	(north)		small proportion
suborder Scolopaci				
superfamily Jacanoidea				
family Jacanidae	warm			most or all
family Rostratulidae	warm			one out of two
superfamily Scolopacoidea				
family Scolopacidae	cold/temp	north	several	several

cies the male's parental care continues after the female departs to her wintering grounds (Myers 1981a, b). In at least two calidridine species (*Calidris alba* and *C. temminckii*) and in the Mountain Plover (*Charadrius montanus*, family Charadriidae) the female may lay two clutches of eggs in quick succession, of which the first will be cared for by her mate and the second by herself (Parmelee 1970, Parmelee & Payne 1973, Gaul 1973, 1975, Hildén 1975). A few clutches of eggs may be laid by the female Dotterel (*Eudromias morinellus*, family Charadriidae: Nethersole-Thomson 1973), which are solely incubated and cared for by males. Paternal care also seems to occur in the Long-toed Stint (*Calidris subminuta*: Myers *et al.* 1982).

In a number of species the social systems seem to be still more extreme than in the Dotterel. These systems are characterized by a complete role reversal between male and female with competition between females and several instances of polyandry (Jenni 1974, Gaul *et al.* 1977, Ridley 1978). They occur in the Spotted Sandpiper (*Actitis macularia*: Hays 1972, Oring & Knudson 1972, Oring & Maxson 1978, Maxson & Oring 1980, Oring 1982) and the phalaropes (Tinbergen 1935, Höhn 1967, 1971, Hildén & Vuolanto 1972, Gilland 1974, Kistchinski 1975) which belong to the family Scolopacidae, and in the related families (Table 1) Jacanidae (Jenni & Collier 1972, Jenni 1974, Jenni & Betts 1978, Stephens 1982) and Rostra-

tulidae (Schmidt 1961, Lowe 1963, Ridley 1978).

It may be concluded that the diversity of social systems within the order Charadriiformes is extremely large. It is not easy to state which kind of organization could have existed in the common ancestor of this order. Nevertheless, knowledge about such a primitive mating system might be important to evaluate the factors responsible for the evolution of recent social systems, such as in the Ruff. Therefore, by means of comparisons between related species, I shall make some inferences about this primitive system.

4. EVOLUTIONARY BASIS

The group of close relatives to the Ruff, subfamily Calidridinae (Voous 1973), comprises 24 species, which all breed in the boreal, subarctic, and arctic regions (Fig. 3). Their range approximately lies north of the 15° July isotherm, mainly coinciding with the area which underground is permanently frozen, and it includes the tundra-zone. Most of this range is only accessible to the birds during their breeding season. Related to this, most species migrate over considerable distances.

The cold habitat was available during only part of the evolution of the Calidridinae (Larson 1957). The genus *Erolia* (synonym *Calidris*) has been described already from the Lower Miocene (Brodkorb 1967). Other fossils classified in

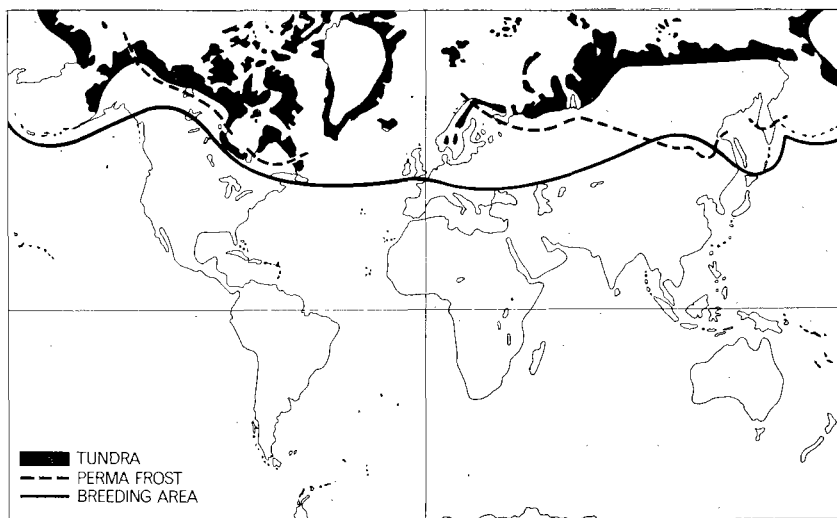


Fig. 3. Tundra areas and the southern borders of the breeding range of Calidridinae (Dement'ev *et al.* 1951, American Ornithologists' Union 1957, Glutz *et al.* 1975, Cramp & Simmons 1983) and of the areas with permanently frozen soils.

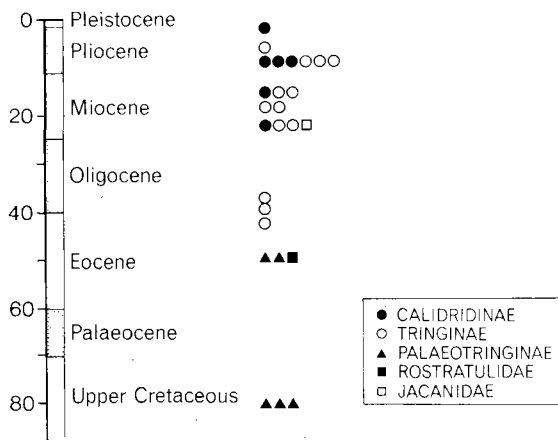


Fig. 4. Fossils of the suborder Scolopaci and their dating in millions of years. Modified from Brodkorb (1967).

the family Scolopacidae (Fig. 4) have even been reported from the Upper Cretaceous (subfamily Palaeotringinae). Most speciation within the Calidridinae must have occurred during the tertiary epochs, which were characterized by a much warmer climate without real tundra areas (Larsen 1957). In the northern hemisphere temperate and cold habitats were scarce, and restricted to the arctic, the northwest American, and the central Asian mountain areas. Thus, it is not self-evident that the common ancestors of Calidridinae were living in cold habitats like their recent descendants. It might be possible, therefore, that these primitive sandpipers were not primarily adapted to breed in a cold climate, but to breed under particular conditions which now mainly occur in cold climates, and which would have occurred in other circumstances.

One of the most likely candidates for such conditions in the present breeding habitats is the sudden emergence of adult Diptera, which may be extremely abundant during a ten-day period every season (Fig. 5). These insects represent the most important food for young calidridine chicks. Hatching of the eggs is mostly synchronized with the start of the period with emerging insects. Such very short, but impressive peaks in the availability of adult Diptera could have occurred in other circumstances, in particular in a swampy environment after seasonal river-floods or rainy periods.

In fact the adult Calidridinae and other Scolopacidae are well adapted to a wet environment

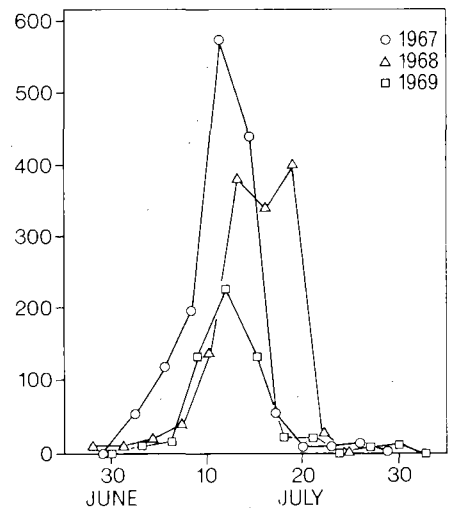


Fig. 5. Total catch per three days of adult crane-flies (Tipulidae) near Barrow, Alaska in three successive seasons after MacLean & Pitelka (1971).

with many invisible prey. Most of these species are marked by relatively long legs suitable for wading, and long bills with numerous minute tactile organs (Herbst corpuscles: Bolze 1968) to localize prey in the soft soil. This foraging method enables the birds to exploit larval arthropods, worms and small molluscs (Burton 1974). Their small precocial self-feeding chicks, however, have to exploit other food resources because their bills are too small to thrust deep enough into the soil. These individuals are mainly dependent on the adult Diptera emerging from the marshes.

In the Arctic (and perhaps also in other areas) Diptera emerge during a very short, but fairly predictable period (Holmes 1970, MacLean & Pitelka 1971). Furthermore there is little time available for preparations, like territory establishment, pair-formation, egg-laying and incubation, prior to insect emergence. I am inclined to think that these two factors, compressed seasons with ample food and minimal preparation periods, were essential for the evolution of Calidridinae and other Scolopacidae. One of the most important features, enabling these birds to exploit such resources, is the role of the male during incubation and care for the chicks, as described in the previous section. This male parental care may be associated with the large costs for the female to produce the eggs,

which precludes her from further parental investment during the short preparation time (Graul 1973, Graul *et al.* 1977; but see also Erckmann 1983).

I want to stress that this association does not necessarily imply that the male's parental care is a derived character evolved in this group of birds to cope with particular ecological conditions. In fact at least three arguments can be given for the alternative that paternal care (as defined by Ridley 1978) is a primitive character within this group of birds. In the first place, in almost all species of the suborder Scolopaci (Table 1) the female is larger than the male (*e.g.* Prater *et al.* 1977). Exceptions to this rule only occur in polygynous and promiscuous species. The dimorphism between large females and small males is most pronounced in species with complete role reversal like Jaçanas (Jenni & Collier 1972), the Painted Snipe *Rostratula benghalensis*, Spotted Sandpiper, and the phalaropes (Prater *et al.* 1977). This suggests that sexual size dimorphism in this group reflects a role differentiation between egg-layers (females) and incubators (males). Egg-layers should be relatively large and be able to store a considerable amount of reserve materials because natural selection has favoured individuals which were able to lay complete clutches, often com-

prising more than 50% of their body weight, within a very short period. Incubators should be relatively small because natural selection has favoured individuals which were able to collect within short interruptions of incubation the large number of small insects to cover their energetic requirements.

In the second place, in almost all species of Scolopaci with biparental care the male stays longer with the chicks than the female, and the male performs the larger portion of parental care after egg-laying (*e.g.* Glutz *et al.* 1975, 1977, Cramp & Simmons 1983). Finally, the third argument for paternal care as a primitive character in Charadriiformes is related to the finding that paternal care and polyandry only occur in a very small number of monophyletic groups of birds (Table 2). It is common in ratite birds (Ridley 1978) which can be classified in one order (Palaeognathiformes: Cracraft 1981). It also occurs in a few species of the order Galliformes (Oring 1982), and in addition in two suborders of Charadriiformes (Table 1) and in the order Gruiformes (Ridley 1978, Oring 1982) which are classified in the same division (Cracraft 1981). On the other hand polygyny is distributed among many more groups of birds. These findings suggest that paternal care and polyandry do not easily originate during evolution. Thus, the high incidence of paternal care within two of the three suborders of the Charadriiformes might be an indication for common descent of the character, instead of the suggestion that the character originated independently in different lineages from shared parental care (Kendeigh 1952, Skutch 1957, Selander 1972, Emlen & Oring 1977, Graul *et al.* 1977, Ridley 1978, Wittenberger 1979, Oring 1982, Erckmann 1983). Consequently I want to take the line of argument that paternal care was one of the options of the common ancestor of the suborders Scolopaci and Charadriomorpha (Table 1) or perhaps of the orders Charadriiformes and Gruiformes or even of all birds (Elzanowski pers. comm., Van Rhijn 1984).

In the subfamily Calidridinae complete role reversal between male and female has not been reported. Myers *et al.* (1982) suggested that the male Long-toed Stint (*Calidris subminuta*) performs all parental care because the female

Table 2. Paternal care in birds after Van Tyne & Berger (1975), Ridley (1978), and Oring (1982). Classification according to Cracraft (1981)

Order family	species with ♂♂ caring broods	number of species in family
Palaeognathiformes (consists of 5 families)		
Tinamidae	most or all	± 45
Apterygidae	all	3
Casuariidae	all	3
Dromiceidae	at least one	2
Rheidae	at least one	2
Galliformes (consists of 5 families)		
Megapodidae	many or all	10
Phasianidae	small proportion	±200
Gruiformes (consists of 11 families)		
Mesornithidae	at least one	3
Turnicidae	many or all	16
Charadriiformes (consists of 16 families)		
Charadriidae	small proportion	± 50
Jacaniidae	most or all	7
Rostratulidae	one	2
Scolopacidae	several	± 85

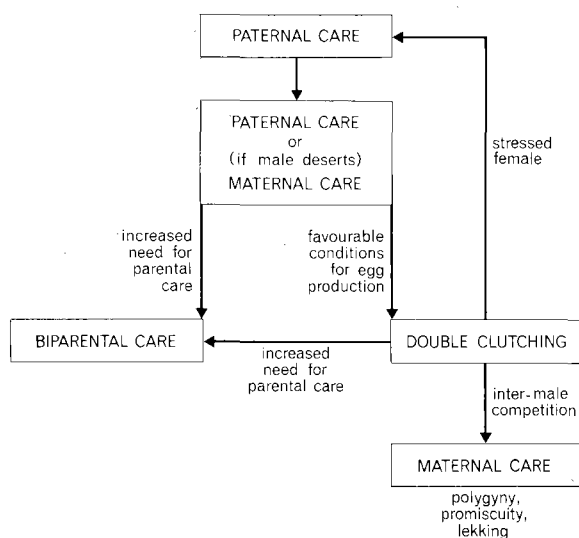


Fig. 6. Some possible pathways for the evolution of parental care and social organization in waders.

seems to depart from the breeding area immediately after egg-laying. This could be the primitive mating strategy within this subfamily (Fig. 6). In such system the survival of clutches might be restricted by a tendency of males to desert their mates before all eggs have been laid (Van Rhijn 1984). Therefore, it is conceivable that natural selection has favoured the development of female care in those cases where the male disappears. Subsequently parental care patterns could have evolved in two different directions (Fig. 6). Firstly, when environmental conditions became too harsh for one parent to incubate the eggs or to protect the chicks sufficiently, females could enlarge their reproductive success by assisting their mates with first clutches. Owing to this, biparental care could have been developed. Secondly, when environmental conditions enabled females to lay more clutches of eggs in succession, they could enlarge their reproductive success by the production of a new clutch after that the care for the previous clutch had been delegated to her mate. Owing to this, the double clutch system could evolve.

The biparental care system occurs in most calidridine species and in many other birds. The double clutch system is far less common, although not exceptional in the Calidridinae. It occurs in the Sanderling (*Calidris alba*: Parmelee 1970, Parmelee & Payne 1973, but see

Pienkowski & Green 1976), Temminck's Stint (Hildén 1975, 1978). Little Stint (*C. minuta*: Kistchinski & Flint 1973), and it may occur in the Dunlin (*C. alpina*: Soikkeli 1967). In these species the first clutch is tended by the male and the second by the female. The start of incubation of the first clutch is postponed until the second is completed. Since all females in the same population start to lay almost synchronously, hatching of the eggs occurs during a very short period. Consequently, this system is perfectly suited for synchronizing hatching of a maximum number of eggs after a short preparation time with the beginning of the period with emerging Diptera.

In fact the double clutch strategy is another likely candidate for the mating system of the common ancestor of Calidridinae (Fig. 6). It is meaningful that all recent social systems which have been described within the subfamily Calidridinae can easily be derived from this assumed primitive mating strategy. The biparental care system, which seems to be the most common breeding strategy (Pitelka *et al.* 1974, Myers 1981a), can be derived from the first clutch in the common ancestor. This development could be related with an increased need for parental care, perhaps by an increased danger of predation, or by the need of almost uninterrupted incubation schedules (Norton 1982, Pienkowski & Green 1976). The male parental care system, such as in the Long-toed Stint, could also be derived from the first clutch. This latter kind of development could be related to harsh breeding conditions, which did not allow the female to lay a second clutch. The female parental care system in polygynous, promiscuous, and lekking species, such as *Calidris fuscicollis*, *C. melanotos*, *C. accuminata*, *C. ferruginea*, *Tryngites subruficollis*, and *Philomachus pugnax*, must be derived from the last clutch in the common ancestor. Natural selection might have favoured females which, for copulations prior to their last clutch, select a male with superior properties contributing to the viability of the offspring, which do not include his caring qualities. This could be accompanied by an increase of inter-male competition for females. When ecological conditions did not allow double clutching any longer, females had to select a male on the basis

of his caring qualities and other properties contributing to the viability of the offspring (first clutch) or only on the basis of these other properties contributing to the viability of the offspring (second clutch). In these cases where the need for extra parental care was absent or small (Maynard Smith 1977), polygynous and promiscuous systems without parental care by the male could develop.

In a system of successive clutches the female should avoid polyandrous matings for the first clutches to be tended by males, because uncertainty about paternity could lead to a selection against male parental care (Trivers 1972). Indeed, in the double clutching Sanderling males and females seem to arrive at the same time in the breeding area (Parmelee 1970). For the first clutch of eggs the monogamous pairbond should predominate. On the other hand, for the second clutch it pays for the female to develop the property of sperm storage, because this enhances the probability of fertilization of the clutch she will tend alone when males may be absent. It also pays for a female to copulate with several males for that clutch, because it promotes the presence of fertile sperm (Beatty 1960, Napier 1961). This prediction seems to be fulfilled too. In the double clutching Temminck's Stint females copulate with a new mate

after their first clutch of eggs (Hildén 1975, Pienkowski & Green 1979).

These considerations imply that fertile sperm from different males may be present in females ready to ovulate for their last clutch of eggs. This allows direct competition between unrelated spermatozoa. Consequences of sperm competition have mainly been studied in insects (Parker 1970, Walker 1980). The scattered data for birds mainly refer to domesticated species (Allen & Champion 1955, Atkinson *et al.* 1966, Lake 1975). Fertilization success of semen from one male in competition with semen from other males appeared to be best correlated with sperm motility (Allen & Champion 1955). The deviating shape of spermatozoa from the Scolopacidae in comparison with other Charadriiformes (Fig. 7) might be related to an evolution of competitive sperm within this family, perhaps by an improvement of sperm motility, although oscine spermatozoa, which in addition possess a helical membrane, display reduced levels of motility (Henley *et al.* 1978).

5. EVOLUTION OF THE RUFF'S SOCIAL SYSTEM

In view of the arguments made in the previous section I here assume that the Ruff's social system evolved from a primitive state with two clutches of eggs in quick succession. This ancestral reproductive strategy enabled females to make two different kinds of choices for mates. For the first clutch, which is associated with a moderate investment by the female (production of eggs), she should primarily select a male with good caring qualities, and, additionally, the male's other properties contributing to the viability of the offspring (fertility of his sperm, genetical properties, etc.) should be as good as possible. Such males will be further labeled with "baby-sitters". For the second clutch, which is associated with a heavy investment by the female (production of eggs, incubation, and tending the offspring), she should select a male with superior properties contributing to the viability of the offspring which are independent of the male's actual caring qualities. Such males will be further labeled with "supermen". It must be noticed, however, that the ancestral mating strategy was only stable as long as the female did not use different criteria for

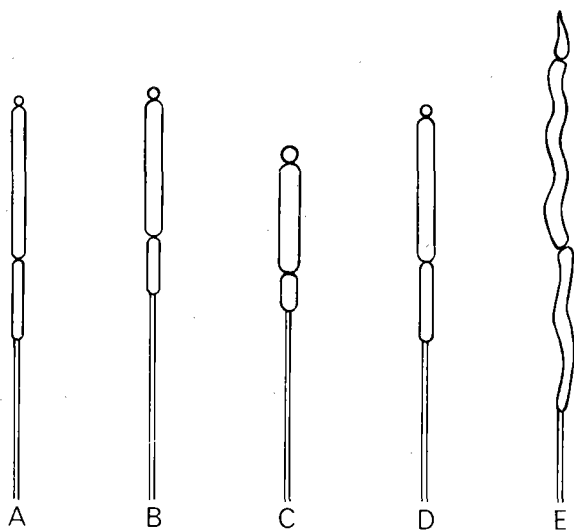


Fig. 7. Spermatozoa from Alcidae (A), Laridae (B), Recurvirostridae (C), Charadriidae (D), and Scolopacidae (E) after McFarlane (1963).

selecting a mate for the first and second clutch. If she did make a distinction between a baby-sitter and a superman, then two different types of males could arise in the population by means of disruptive selection. A typical baby-sitter, however, did not succeed to fertilize more than the one clutch of eggs he would tend himself, while the typical supermen were able to fertilize all clutches to be tended by females. As long as the number of clutches tended by females exceeded the number of supermen, a superman was able to fertilize on the average more than one clutch of eggs, and thus more than a baby-sitter. Consequently the proportion of supermen would rise in the population. If all females were strongly inclined to tend one clutch of eggs and if the number of laying females was equal or larger than the number of males, then the baby-sitters should become extinct. The evolution of polygynous and promiscuous systems, as discussed in the previous section, could be initiated in this way.

It is obvious that the equilibrium in a system with baby-sitters and supermen is very delicate. Only a slight change in the sex-ratio or in the ability of females to care for their own clutches might lead to the extinction of baby-sitters. Anyhow a number of factors may contribute to the fixation of the baby-sitter type in the population. In the first place, the possibility that fertile sperm may be stored for a considerable time by the female, could indicate that baby-sitters fertilize some second clutches to be tended by females, and thus that their success is higher than one clutch per male. Secondly, if baby-sitters transfer a more appropriate genotype for parental care than supermen to their daughters, then the baby-sitter type may be maintained because their daughters raise more offspring than other females. Finally, it is conceivable that baby-sitters change their strategy and steal copulations without taking part in inter-male aggression, and perhaps in a later stage even without taking part in parental care. A stable equilibrium could then be established in the population between a majority of aggressive and a minority of sneaky non-aggressive males (Selander 1965, Gadgil & Bossert 1970, Gadgil 1972).

In the Ruff's social system the role differentiation between independent and satellite

males reminds of a system with supermen and highly modified baby-sitters. It is likely that independent males may be equivalent to competitors or supermen. Although satellites do not show any parental behaviour, they display at least two characters which may be connected with a baby-sitter strategy for the first clutches which are laid in the population. In the first place, satellites often associate with female flocks (Van Rhijn 1983), which could be related to the finding that in double clutching species males and females seem to arrive at the same time in their breeding areas. Secondly, satellite males copulate on the average earlier in the season than independent males (Van Rhijn 1973).

Assuming that the hypotheses about descent were true, then I still have to explain why, in the first stages of evolution of the Ruff's social system, the baby-sitter strategy survived until it became more specialized. My present view is that the breeding area of the ancestral species included a broad range of ecological conditions. In the north of this range lek display of males was strongly limited because the high energetic requirements could not easily be covered by the local food conditions. Consequently, in the north the baby-sitter types were able to expel the supermen. In the south of their range, however, ecological conditions were excellent for lek behaviour. Consequently the success of baby-sitters in those regions was extremely small.

Every year the southern populations were visited by a large number of males and females migrating to the north. Thus northern females had the opportunity to mate with a superman on the southern leks. Similarly, southern males had the opportunity to mate with extra northern females. However, when trying to attract extra females, the southern males had to compete with the northern ones which were accompanying their partners and would try to prevent extra-marital copulations. One possibility to attract these migrating females towards the leks of local males, was also to attract the partners of these females: the migrating baby-sitters. One possibility to attract these males was to give them a share in the copulations. This is almost exactly what happens with satellites on a lek. Furthermore, satellites do play the role of link between female flocks and leks (Van Rhijn

1983). Finally, the evolution of a temporal and spatial segregation between copulation and egg-laying follows from these ideas.

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7. SUMMARY

In order to explore the phylogenetical roots, the known facts and provisional deductions about the unique social system of the Ruff have been considered against a background of data on social systems within the subfamily Calidridinae, the family Scolopacidae, the suborder Scolopaci, and the order Charadriiformes. The Ruff's social system is characterized by lek behaviour, role differentiation between independent and satellite males, and possibly by a temporal and spatial segregation between copulation and fertilization. Such social system has never been described for related species. Only the property to display on leks has been demonstrated in a few of them.

In fact the group of waders is marked by an enormous diversity of mating systems. I consider all these strategies to be derived from a system which was adapted to exploit compressed peaks in the availability of food for chicks. Likely candidates for such common ancestral system are male care systems and "double clutch" strategies.

It is argued that the Ruff's behavioural dimorphism among males might have been originated by disruptive selection in a double clutch system. Satellites are thought to be derived from males selected to care for offspring; independent males from those selected to compete for additional copulations.

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9. SAMENVATTING

Het is vrijwel onmogelijk om harde gegevens in handen te krijgen over het gedrag en de sociale organisatie van al lang geleden uitgestorven vogelsoorten. Toch lijkt het aannemelijk, dat er redelijk betrouwbare reconstructies van het sociale gedrag van de voorouders van onze huidige vogelsoorten gemaakt kunnen worden, door zorgvuldige vergelijkingen tussen soorten, van welke — op grond van andere gegevens — hypothesen over fylogenetische verwantschappen zijn opgesteld. In dit artikel worden de bekende feiten en voorlopige conclusies over het sociale systeem van de Kemphaan geplaatst tegen een achtergrond van gegevens over gedrag van verwanten binnen de subfamilie, de familie, de suborde en de orde waartoe de Kemphaan behoort.

Het sociale systeem van de Kemphaan wordt gekenmerkt door baltsgedrag en arena's (leks), door de sterk verschillende rolpatronen die door waarschijnlijk genetisch niet identieke categorieën van mannen worden vervuld, en mogelijk door een scheiding in ruimte en tijd tussen copulatie en bevruchting van de eicel. Een dergelijk sociaal systeem is niet eerder beschreven voor een verwante soort. Alleen de eigenschap van het vertoon van baltsgedrag op arena's is aangetoond voor een aantal soorten binnen dezelfde familie.

Binnen de groep van steltlopers komt een enorme verscheidenheid voor van paarvormingssystemen. Al die systemen zijn volgens mij afgeleid van een voorouderstrategie die aangepast was aan het benutten van kort durende pieken in de beschikbaarheid van voedsel voor kuikens. Binnen een dergelijk raamwerk zouden de eveneens in dezelfde vogelgroep aangetroffen vaderzorg-systemen en dubbel-legsel-systemen heel goed kunnen passen.

Met betrekking tot het sociale systeem van de Kemphaan is beargumenteerd dat de verschillende rolpatronen van mannen ontstaan kunnen zijn door een selectie in twee richtingen, die plaats kon vinden tijdens een fase met een dubbel-legsel-systeem. Satellieten zouden dan afgeleid zijn van mannen die in eerste instantie uitgeselecteerd waren voor het optimaal vervullen van ouderzorg; onafhankelijke mannen van individuen die door selectie gespecialiseerd waren in het verrichten van zoveel mogelijk extra copulaties.